

Association of epaxial musculature with dorsal-fin pterygiophores in acanthomorph fishes, and its phylogenetic significance

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SYNOPSIS. A survey of acanthomorphs reveals that *epaxialis* attachments to distal radials or the distal tips of proximal-middle pterygiophores have a relatively restricted distribution. Four basic morphotypes are recognized: Type 0 – no distal insertions of *epaxialis* (lampridiforms, polymixiiforms, basal paracanthopterygians, zeiforms, beryciforms, smegmamorphs, pleuronectiforms and many perciforms); Type 1 – partially separate *epaxialis* slip(s) inserting on to dorsoposterior and dorsolateral processes of proximal-middle and/or distal radials (batrachoidids [Paracanthopterygii], scorpaeniforms, and among perciforms in blennioids, most cirrhitoids, apogonids, centrogeiniids, latine centropomids, grammatids, haemulids, percids, serranids, champsodontids and cheimarrichthyids); Type 2 – insertions of *epaxialis* to distal portions of pterygiophores without separate slips (possibly basal tetraodontiforms, various perciform taxa including callionymoids, notothenioids, zoarcoids, and some cirrhitids, labrids, percoids and trachinoids); Type 3 – completely separate slip of muscle dorsal to the main body of the *epaxialis* inserting on to anterior pterygiophore shaft with dorsal insertions on to more posterior spine-bearing pterygiophores, and the first ray-bearing pterygiophore, then becoming continuous with the *supracarinalis posterior* (percoid family Mullidae). Type 0 is considered to be plesiomorphic, and the remaining morphologies apomorphic. Their phylogenetic significance is discussed in the context of other characters. Among our conclusions, the Scorpaeniformes is awarded subordinal status within the Perciformes, and the centropomid Latinae is given full familial status.

INTRODUCTION

Within the last five years, there has been renewed interest in higher relationships among acanthomorphs. The recent publication of the Symposium on Phylogeny of Percomorpha (Johnson & Anderson, 1993) and other contributions (Stiassny, 1990; Stiassny & Moore, 1992) have shifted the focus somewhat from phylogenetic work on individual families to broader studies involving interrelationships of suborders and orders. Such studies are hampered by the difficulties inherent in examining large numbers of taxa, determining appropriate character complexes, and interpreting homologies among the variation within those complexes. In many instances, characters are too complex or difficult to survey resulting in an incomplete understanding of their distribution within the included groups. During the course of investigations on the relationships among pseudochromoids (sensu Mooi, 1990), we began surveying the relation of dorsal epaxial myology to the dorsal-fin pterygiophores. Dorsal epaxial myology appears to exhibit limited but sufficient variation over a broad range of taxa and the character states are simple enough to suggest it to be of high potential for phylogenetic analysis of higher relationships among acanthomorphs.

Epaxial muscles, the dorsal component of the body musculature, have received little attention from fish systematists. Although some studies have used variation in the anterior insertions of epaxial slips on to the head (e.g., Mooi, in press;

Stiassny, 1990), few workers using myological features have surveyed this muscle group (Winterbottom, 1974a for a review). Mok *et al.* (1990) were the first to report variation in the relationship of the epaxial musculature with the dorsal-fin pterygiophores. They found that in two percoid families, the Grammatidae and Opistognathidae, the epaxial muscles insert on to the distal portions of anterior dorsal-fin pterygiophores, and interpreted this as evidence for uniting the two taxa as sister groups.

Our continuing studies on the phylogenetic positions of the Grammatidae, Opistognathidae and other pseudochromoid families have failed to provide corroborating evidence for a sister-group relationship between the Grammatidae and Opistognathidae. Moreover, a preliminary survey of epaxial morphology in perciforms revealed that the reportedly unique association of epaxial musculature with dorsal-fin pterygiophores described by Mok *et al.* (1990) is more widely distributed (Gill & Mooi, 1993: 333). Here we present an extensive survey of acanthomorph taxa, and show that, despite having a wider distribution than indicated by Mok *et al.*, epaxial muscle/dorsal-fin pterygiophore associations nevertheless appear to be relatively restricted within acanthomorphs, and exhibit a number of recognizable morphologies. We explore the possible phylogenetic significance of the distribution of epaxial muscle insertions to dorsal-fin pterygiophores and their homology.

METHODS AND MATERIALS

Epaxial musculature/dorsal-fin pterygiophore associations were studied in alcohol-stored specimens. An incision was made through the skin along the length of the fish between one third to one half the distance from the base of the dorsal fin and the midlateral septum. The incision ran from the skull to beneath the segmented-ray portion of the dorsal fin. The skin was either removed or folded dorsally to expose the underlying muscle. The *inclinatores dorsales* usually lifted up with the skin, or were removed individually to permit examination of the epaxial muscles and the dorsal portions of the pterygiophores. When appropriate, epaxial fibres were traced anteriorly or posteriorly to ascertain their association with the *supracarinalis* muscle system. The insertions of epaxial fibres to pterygiophores were often re-examined on cleared and stained specimens and dry skeletons in the collections of the American Museum of Natural History, Milwaukee Public Museum, National Museum of Natural History, and The Natural History Museum. These specimens are not listed in Table 1. Illustrations of muscles were made with a camera lucida attached to a binocular dissecting microscope.

Material dissected for myological observations is listed in Table 1. All species examined during the study are represented in this list, although in many cases, multiple specimens were examined, occasionally from different lots, and sometimes from museum collections other than those listed, particularly the Field Museum of Natural History and Royal Ontario Museum. A complete list can be provided by the authors. Institutional codes follow Leviton *et al.* (1985).

RESULTS

Many (if not most) fishes have some epaxial fibre insertion near the proximal ends or near the middle of the dorsal-fin pterygiophores, whereas some taxa have epaxial muscle insertions on to the distal ends of the pterygiophores. We recognize four morphotypes of epaxial musculature, Types 0 to 3. The consecutive numbering of the morphological types is not meant to imply character transformations; the morphotypes do not necessarily form a polarized transformation series. The vast majority of acanthomorph fishes (including putative basal taxa) exhibit an apparently primitive condition of the epaxial muscles, Type 0, with no attachment to the distal parts of the dorsal-fin pterygiophores, and with the musculature usually lying well below the dorsal tips of the pterygiophores (Fig. 1; Table 1).

Of those taxa that do exhibit insertions on to the distal portions of the pterygiophores, epaxial fibres rarely insert on to pterygiophores other than those bearing non-segmented rays (spines), except where these ray elements are interpreted as secondarily derived from spines (e.g., pseudochromids, zoarcoids, pleuronectiforms). In one scorpaeniform and a perciform genus as discussed below, and probably the paracanthopterygian *Opsanus beta*, there is insertion on primary ray-bearing pterygiophores. Among the taxa with dorsal insertions of epaxial fibres to spine-bearing pterygiophores, there are three recognizable morphologies. Although these morphologies can be defined by specific taxa, their

apparent differences become somewhat subjective at the ends of their respective morphological spectra.

Type 1 is characterized by a partially separate muscle mass or series of slips of muscle fibres that insert on to the dorsoposterior and dorsolateral processes of the proximal-middle and/or distal radials of the pterygiophores. At least some fibres originate from the main body of epaxial muscle, but in extreme cases the dorsal muscle mass is detached between successive myosepta, and anteriorly there can be an elongate separate slip of muscle to an anterior pterygiophore (Fig. 2). We observed this morphotype in a single paracanthopterygian species (*Opsanus beta*) (Fig. 3), blennioids, most cirrhitoids, seven percoid families (Apogonidae, Centrogeniidae, Centropomidae, Grammatidae, Haemulidae, Percidae, and Serranidae) and two trachinoid families (Champsodontidae and Cheimarrichthyidae) among the surveyed perciforms (Figs 1, 4–5, 12–17), and all but one examined scorpaeniform (Figs 6–8) (Table 1).

Among examined scorpaeniforms with Type 1, *Normanichthys crockeri* exhibits a unique morphology (Fig. 8). The epaxial muscles insert on to the lateral processes of the first nine or ten pterygiophores as a separate mass of muscle. Posterior to the first dorsal fin, epaxial fibres attach directly to spineless (naked) pterygiophores and these fibres are not arranged as a separate muscle mass. A separate muscle mass is also present at the second dorsal fin, with insertions on to those pterygiophores bearing segmented rays. This gradually tapers out posteriorly and merges with the main body of epaxial muscle. Other scorpaeniform and percoid taxa exhibiting Type 1 are quite consistent in their epaxial morphology; even among unusual taxa such as *Aploactis* (a scorpaeniform), which has its dorsal fin placed far anteriorly over the skull, a narrow tendon extends from the epaxial to insert on to the third dorsal-fin pterygiophore. Differences arise in the degree of muscle separation, size of the anterior slip, on to which pterygiophores the muscle inserts, and on to which radials of the pterygiophores the insertion occurs (cf. Figs 2–8).

Species with a Type 2 epaxial morphology lack the obvious separation of the dorsal muscle bundle that inserts on to the distal portions of the pterygiophores, and the anterior slip is always absent. The insertions resemble sheets hanging on a clothes-line, draping from one pterygiophore to the next (Fig. 9). In some taxa, the insertions are primarily via long tendons, and the muscle fibres themselves are relatively distant from the dorsal parts of the pterygiophores (Fig. 10). In most elongate taxa, the muscles are much more dorsally situated and the tendons are not as obvious. This morphology is found in various perciform taxa, including some members of the Cirrhitidae, Labridae, Percoidei, and Trachinoidei, and all of the few examined members of the Callionymoidei, Notothenioidei and Zoarcoidei (Table 1). The Tetraodontiformes have a modified condition of this basic morphology which will be discussed below.

A Type 3 epaxial morphology was found only in the family Mullidae (Fig. 11; Table 1). This type consists of a few epaxial fibres inserting on to an anterior pterygiophore relatively ventrally and on to a lateral wing along the main shaft rather than on to a dorsal posterolateral process. A completely separate slip of muscle sits dorsal to the epaxial muscle and inserts on to the anterior pterygiophore and only the posterior pterygiophores of the first dorsal fin. It extends further posteriorly, inserting on to the first pterygiophore of the second dorsal, and gradually narrows posteriorly, insert-

Table 1 List of taxa examined for epaxial muscle morphology. Morphological types: 0 – no association with distal tips of dorsal-fin pterygiophores; 1 – partially separate muscle block or series of slips of muscle fibers that insert on to the dorsoposterior and dorsolateral processes of the proximal-middle and/or distal radials of the dorsal-fin pterygiophores; 2 – insertions to the distal portions of the pterygiophores without an obvious separation from the main muscle body and with no separate anterior slip; 3 – completely separate slip of muscle dorsal to the main body of the *epaxialis* inserting on to an anterior pterygiophore shaft with dorsal insertions on to more posterior spine-bearing pterygiophores and the first pterygiophore bearing a segmented ray, then becoming continuous with the *supracarinalis posterior*. Orders are listed phylogenetically following Johnson & Patterson (1993); suborders, families, and species are listed alphabetically within orders. *Incertae sedis* genera of Percoidei are listed alphabetically among families.

| Taxon, Catalogue No., SL (mm) | Type | Taxon, Catalogue No., SL (mm) | Type |
|--|------|--|------|
| LAMPRIDIFORMES | | Poeciliidae | |
| Veliferidae | | <i>Poecilia mexicana</i> , MPM 8283, 55.4 | 0 |
| <i>Velifer hypselopterus</i> , AMNH 49575, 118.0 | 0 | DACTYLOPTERIFORMES | |
| POLYMIXIIFORMES | | Dactylopteridae | |
| Polymixiidae | | <i>Dactylopterus volitans</i> , USNM 307210, 59.5 | 0 |
| <i>Polymixia lowei</i> , AMNH 10116, 131.0 | 0 | PERCIFORMES | |
| PARACANTHOPTERYGII | | Acanthuroidei | |
| Aphredoderidae | | Acanthuridae | |
| <i>Aphredoderus sayanus</i> , AMNH 50907, 53.5 | 0 | <i>Acanthurus triostegus</i> , USNM 139750, 73.5 | 0 |
| Batrachoididae | | Ephippidae | |
| <i>Opsanus beta</i> , AMNH 52369, 115.0 | 1 | <i>Chaetodipterus zonatus</i> , USNM 131415, 48.9 | 0 |
| Brotulidae | | Scatophagidae | |
| <i>Dinematichthys</i> sp., USNM 297347, 88.5 | 0 | <i>Scatophagus argus</i> , BMNH 1976.4.13:2–7, 48.3 | 0 |
| Gadidae | | Anabantoidei | |
| <i>Urophycis floridanus</i> , MPM 8409, 76.6 | 0 | Anabantidae | |
| Lotidae | | <i>Anabas testudineus</i> , AMNH 13766, 65.0 | 0 |
| <i>Lota lota</i> , MPM 28380, 100.0 | 0 | Badidae | |
| Percopsidae | | <i>Badis badis</i> , USNM 89076, 26.8 | 0 |
| <i>Percopsis omiscomaycus</i> , MPM 14060, 77.1 | 0 | Belontiidae | |
| ZEIFORMES | | <i>Belontia signata</i> , USNM uncat., 64.4 | 0 |
| Parazenidae | | <i>Macropodus opercularis</i> , AMNH 10641, 38.7 | 0 |
| <i>Parazen pacificus</i> , AMNH 29459, 116.5 | 0 | Channidae | |
| BERYCIFORMES | | <i>Channa arga</i> , AMNH 79406, 121.0 | 0 |
| Holocentridae | | <i>C. obscurus</i> , FMNH 70260, 136.0 | 0 |
| <i>Myripristis pralinus</i> , USNM 285922, 113.5 | 0 | Nandidae | |
| <i>Sargocentron vexillarius</i> , MPM 30099, 56.7 | 0 | <i>Monocirrhus polyacanthus</i> , USNM uncat., 68.0 | 0 |
| Trachichthyidae | | <i>Nandus nebulosus</i> , USNM 230323, 47.7 | 0 |
| <i>Hoplostethus mediterraneus</i> , AMNH 49700, 117.0 | 0 | <i>Polycentrus schomburgki</i> , USNM 226071, 41.7 | 0 |
| SYNBRANCHIFORMES | | Pristolepididae | |
| Mastacembelidae | | <i>Pristolepis fasciata</i> , USNM 305711, 75.7 | 0 |
| <i>Caecomastacembelus congricus</i> , AMNH 6157, 145.0 | 0 | Blennioidae | |
| <i>Mastacembelus armatus</i> , FMNH 68484, 190.0 | 0 | Blenniidae | |
| ELASSOMATIFORMES | | <i>Entomacrodus nigricans</i> , MPM 18256, 55.4 | 1 |
| Elassomatidae | | <i>Hyleurochilus aequipinnis</i> , MPM 23034, 28.2 | 1 |
| <i>Elassoma okefenokee</i> , MPM 28810, 20.5 | 0 | <i>Ophioblennius atlanticus</i> , MPM 24880, 52.4 | 1 |
| <i>E. zonatum</i> , MPM 14480, 28.5 | 0 | <i>Scartella cristata</i> , MPM 18231, 62.0 | 1 |
| GASTEROSTEIFORMES | | Chaenopsidae | |
| Aulostomatidae | | <i>Acanthemblemaria greenfieldi</i> , MPM 24876, 30.4 | 1 |
| <i>Aulostomus maculatus</i> , MPM 25182, 174.2 | 0 | <i>A. aspera</i> , MPM 29983, 24.7 | 1 |
| Aulorhynchidae | | <i>Emblemaria pandionis</i> , BMNH 1938.2.2:2, 39.3 | 1 |
| <i>Aulorhynchus flavidus</i> , AMNH 58939, 123.0 | 0 | <i>Stathnonotus gymnodermis</i> , MPM 24881, 23.6 | 1 |
| Gasterosteidae | | <i>S. stahli</i> , BMNH 1939.5.12:183–189, 18.8 | 1 |
| <i>Culaea inconstans</i> , MPM 26675, 50.2 | 0 | Clinidae | |
| <i>Gasterosteus aculeatus</i> , AMNH 37959, 54.0 | 0 | <i>Clinoporus biporosus</i> , BMNH 1935.4.29:1–8, 89.5 | 1 |
| Macrorhamphosidae | | <i>Clinus cottoides</i> , BMNH 1887.4.16:3–5, 93.0 | 1 |
| <i>Macrorhamphosus scolopax</i> , AMNH 84458, 85.5 | 0 | Dactyloscopidae | |
| MUGILIFORMES | | <i>Dactyloscopus tridigitatus</i> , MPM 24981, 60.0 | 1 |
| Mugilidae | | <i>Gillellus uranidea</i> , MPM 30131, 29.5 | 1 |
| <i>Agonostomus monticola</i> , MPM 13806, 41.0 | 0 | Labrisomidae | |
| <i>Mugil cephalus</i> , USNM 152118, 93.2 | 0 | <i>Labrisomus bucciferus</i> , MPM 31163, 57.0 | 1 |
| <i>M. curema</i> , MPM 6817, 56.4 | 0 | <i>L. nuchipinnis</i> , MPM 18253, 82.0 | 1 |
| ATHERINIFORMES | | <i>Malacotenus gilli</i> , MPM 24947, 49.1 | 1 |
| Atherinidae | | <i>M. versicolor</i> , MPM 22469, 36.0 | 1 |
| <i>Atherinomorbus stipes</i> , MPM 30102, 53.4 | 0 | <i>M. zonifer</i> , BMNH 1861.8.13:33, 47.3 | 1 |
| <i>Menidia beryllina</i> , MPM 30404, 63.0 | 0 | <i>Paraclinus fasciatus</i> , MPM 25004, 36.2 | 1 |
| CYPRINODONTIFORMES | | <i>Starksia lepicoelia</i> , MPM 29994, 23.5 | 1 |
| Cyprinodontidae | | Tripterygiidae | |
| <i>Cyprinodon variegatus</i> , MPM 28940, 45.6 | 0 | <i>Enneanectes atrorus</i> , MPM 30216, 21.0 | 1 |
| Fundulidae | | <i>E. boehlkei</i> , MPM 11572, 18.2 | 1 |
| <i>Fundulus catenatus</i> , MPM 15271, 70.8 | 0 | <i>E. pectoralis</i> , MPM 22463, 26.5 | 1 |
| | | <i>Lepidoblennius haplodactylus</i> , BMNH 1890.9.23, 63.6 | 1 |

| Taxon, Catalogue No., SL (mm) | Type | Taxon, Catalogue No., SL (mm) | Type |
|--|------|--|------|
| Callionymoidei | | Percoidei | |
| Callionymidae | | Acropomatidae | |
| <i>Synchiropus splendidus</i> , MPM uncat., 59.2 | 2 | <i>Malakichthys griseus</i> , USNM 184143, 60.2 | 0 |
| Gobiesocidae | | Ambassidae | |
| <i>Gobiesox strumosus</i> , AMNH 86887, 58.5 | 0 | <i>Ambassis</i> sp., USNM 223376, 37.8 | 0 |
| Carangoidei | | <i>Chanda ranga</i> , BMNH 1938.12.22:132-141, 40.0 | 0 |
| Carangidae | | Apogonidae | |
| <i>Caranx latus</i> , MPM 13771, 119.0 | 0 | <i>Apogon angustatus</i> , USNM 261750, 57.0 | 1 |
| <i>Oligoplites saurus</i> , MPM 6364, 77.2 | 0 | <i>Apogonichthys ocellatus</i> , AMNH 33808, 43.0 | 1 |
| <i>Selene vomer</i> , MPM 2273, 75.1 | 0 | <i>Cheilodipterus macrodon</i> , AMNH 33714, 68.0 | 1 |
| <i>Trachinotus rhodopus</i> , MPM 6369, 107.0 | 0 | Bathyclupeidae | |
| Nematistiidae | | <i>Bathyclupea malayana</i> , BMNH 1982.9.6:106-107, 117.0 | 0 |
| <i>Nematistius pectoralis</i> , MPM 6367, 215.0 | 0 | Callanthiidae | |
| Cirrhitidae | | <i>Callanthias australis</i> , AMS I.18709-002, 88.0 | 0 |
| Aplodactylidae | | <i>C. platei</i> , USNM 307594, 93.0 | 0 |
| <i>Aplodactylus punctatus</i> , USNM 227298, 58.0 | 1 | Caproidae | |
| Cheilodactylidae | | <i>Antigonia eos</i> , MPM 13598, 71.3 | 0 |
| <i>Cheilodactylus variegatus</i> , USNM 77574, 58.0 | 1 | <i>Capros aper</i> , BMNH 1963.5.14:230-239, 43.5 | 0 |
| <i>C. zonatus</i> , USNM uncat., 73.5 | 1 | Centrarchidae | |
| Chironemidae | | <i>Lepomis gibbosus</i> , MPM 28675, 56.2 | 0 |
| <i>Chironemus marmoratus</i> , ROM 40360, 125.4 | 1 | <i>Micropterus salmoides</i> , MPM 20246, 62.2 | 0 |
| Cirrhitidae | | Centrogeniidae | |
| <i>Amblycirrhitus bimacula</i> , MPM 13509, 56.9 | 2 | <i>Centrogenys vaigensis</i> , USNM 245612, 70.0 | 1 |
| <i>Cirrhitichthys oxycephalus</i> , ROM 60291, 55.2 | 1 | Centropomidae | |
| <i>Cirrhitops hubbardi</i> , ROM 59830, 64.5 | 2 | <i>Centropomus armatus</i> , USNM uncat., 108.7 | 0 |
| <i>Cirrhitus pinnulatus</i> , ROM 47702, 101.0 | 2 | <i>C. ensiferus</i> , ROM 61657, 47.7 | 0 |
| <i>Neocirrhitus armatus</i> , ROM 59838, 44.1 | 1 | <i>C. pectinatus</i> , ROM 61664, 61.0 | 0 |
| <i>Paracirrhitus arcatus</i> , MPM 13587, 66.7 | 1 | <i>C. undecimalis</i> , ROM 40904, 118.5 | 0 |
| Gobioidei | | Cepolidae | |
| Butidae | | <i>Cepola rubescens</i> , BMNH 1970.4.18:3, 438.0 | 2 |
| <i>Butis amboinensis</i> , MPM uncat., 57.2 | 0 | <i>Owstonia totomiensis</i> , BMNH 1986.10.6:61, 91.0 | 2 |
| Eleotrididae | | Chaetodontidae | |
| <i>Eleotris pisonis</i> , USNM 314448, 77.5 | 0 | <i>Chaetodon multicinctus</i> , MPM 13556, 89.7 | 0 |
| Gobiidae | | <i>C. miliaris</i> , MPM 13466, 56.0 | 0 |
| <i>Awaous taiasica</i> , MPM 6811, 92.1 | 0 | <i>Datnioides quadrifasciatus</i> , USNM 297256, 120.0 | 0 |
| <i>Bathygobius soporator</i> , MPM 18232, 80.0 | 0 | Dinolestidae | |
| Odontobutidae | | <i>Dinolestes lewinii</i> , USNM 59932, 138.5 | 0 |
| <i>Micropercops</i> sp., AMNH 10441, 44.4 | 0 | Enoplosidae | |
| Xenisthmidae | | <i>Enoplosus armatus</i> , USNM 48808, 77.5 | 0 |
| <i>Xenisthmus balius</i> , USNM 326758, 26.1 | 0 | Gerreidae | |
| Labroidei | | <i>Eucinostomus gula</i> , USNM 43216, 45.0 | 0 |
| Cichlidae | | Glaucosomatidae | |
| <i>Cichlasoma salvini</i> , MPM 22851, 48.8 | 0 | <i>Glaucosoma scapulare</i> , AMS I.27325-002, 45.1 | 0 |
| <i>Etioplos suratensis</i> , USNM 301169, 69.5 | 0 | Grammatidae | |
| Embiotocidae | | <i>Gramma linki</i> , AMNH 35776, 36.3 | 1 |
| <i>Rhacochilus argyrosomus</i> , USNM 53969, 45.7 | 0 | <i>G. loreto</i> , MPM 15612, 50.4 | 1 |
| Labridae | | <i>Lipogramma anabantoides</i> , AMNH 33061, 16.8 | 1 |
| <i>Bodianus bilunulatus</i> , MPM 13518, 76.3 | 0 | <i>L. trilineata</i> , FMNH 95658, 24.2 | 1 |
| <i>B. diana</i> , USNM 232355, 52.0 | 0 | Haemulidae | |
| <i>Cheilinus oxycephalus</i> , USNM 262088, 62.1 | 2 | <i>Anisotremus scapularis</i> , USNM 127982, 55.8 | 1 |
| <i>Cheilio inermis</i> , MPM 13369, 88.6 | 2 | <i>Conodon nobilis</i> , MPM 13778, 104.5 | 1 |
| <i>Choerodon graphicus</i> , USNM 218548, 60.2 | 0 | <i>Haemulon aurolineatum</i> , MPM 23228, 64.2 | 1 |
| <i>Coris variegata</i> , USNM uncat., 86.0 | 2 | <i>Hapalogenys</i> sp., BMNH 1984.1.13:76-82, 55.0 | 0 |
| <i>Halichoeres bivittatus</i> , MPM 8524, 73.6 | 2 | <i>Hemilutjanus microphthalmus</i> , USNM 77623, 138.0 | 0 |
| <i>Hemipteronotus martinicensis</i> , USNM 37075, 85.0 | 2 | Kuhliidae | |
| <i>Labroides dimidiatus</i> , MPM uncat., 51.7 | 2 | <i>Kuhlia rupestris</i> , USNM 184110, 82.0 | 0 |
| <i>Sparisoma rubripinnis</i> , MPM 30040, 62.6 | 2 | Kurtidae | |
| <i>Tautoga onitis</i> , USNM 118352, 53.2 | 0 | <i>Kurtus gulliveri</i> , USNM 217310, 128.0 | 0 |
| <i>Thalassoma duperryi</i> , MPM 13403, 77.7 | 2 | Kyphosidae | |
| <i>T. lutescens</i> , USNM 112696, 82.0 | 2 | <i>Girella tricuspidata</i> , USNM 269547, 99.5 | 0 |
| Pomacentridae | | <i>Sectator oxyurus</i> , USNM 288880, 75.1 | 0 |
| <i>Abudefduf saxatilis</i> , USNM 275040, 63.5 | 0 | Lactariidae | |
| <i>Amphiprion melanopus</i> , USNM 309519, 68.0 | 0 | <i>Lactarius delicatulus</i> , BMNH 1895.2.28:51, 87.0 | 0 |
| <i>Lepidozygus tapeinosoma</i> , USNM 275893, 51.5 | 0 | <i>Lateolabrax japonicus</i> , USNM 64630, 87.0 | 0 |
| Notothenioidei | | Latidae | |
| Nototheniidae | | <i>Lates albertianus</i> , ROM 26537, 141.1 | 1 |
| <i>Notothenia sima</i> , AMNH 5003, 82.5 | 2 | <i>L. calcarifer</i> , BMNH 1898.12.24:2, 113.5 | 1 |
| | | <i>L. mariae</i> , ROM 28140, 125.2 | 1 |
| | | <i>L. niloticus</i> , BMNH 1907.12.2:2959-2968, 48.5 | 1 |

| Taxon, Catalogue No., SL (mm) | Type | Taxon, Catalogue No., SL (mm) | Type |
|---|------|---|------|
| <i>Psammoperca waigiensis</i> , BMNH 1933.3.11:312, 118.0 | 1 | <i>Bairdiella chrysur</i> , MPM 8954, 100.0 | 2 |
| Lethrinidae | | <i>Cynoscion regalis</i> , MPM 8969, 94.9 | 2 |
| <i>Lethrinus lentian</i> , BMNH 1932.7.29:82–83, 70.8 | 0 | <i>Equetus acuminatus</i> , MPM 8522, 90.1 | 2 |
| Lobotidae | | <i>Leiostomus xanthurus</i> , MPM 8934, 87.1 | 0 |
| <i>Lobotes surinamensis</i> , USNM 156452, 46.6 | 0 | <i>Menticirrhus litoralis</i> , MPM 8443, 68.7 | 2 |
| Lutjanidae | | <i>Micropogonias undulatus</i> , USNM 142675, 67.5 | 0 |
| <i>Lutjanus griseus</i> , MPM 8542, 48.1 | 0 | <i>Sciaenops ocellata</i> , MPM 30424, 61.5 | 2 |
| <i>L. kasmira</i> , USNM 183109, 98.8 | 0 | <i>Stellifer lanceolatus</i> , MPM 8936, 57.9 | 2 |
| Malacanthidae | | Serranidae | |
| <i>Caulolatilus affinis</i> , USNM 211424, 104.5 | 0 | <i>Alphestus afer</i> , USNM 235696, 89.0 | 1 |
| Monodactylidae | | <i>Anyperodon leucogrammus</i> , USNM uncat., 103.5 | 1 |
| <i>Monodactylus argenteus</i> , MPM 31026, 33.2 | 0 | <i>Centropristis philadelphicus</i> , USNM 142813, 75.8 | 1 |
| Moronidae | | <i>Chelidoperca</i> sp., USNM 322386, 80.0 | 1 |
| <i>Dicentrarchus labrax</i> , BMNH 1987.2.22:1–12, 42.5 | 0 | <i>Diplectrum macropoma</i> , USNM 211397, 129.0 | 1 |
| <i>Morone chrysops</i> , MPM 4569, 78.3 | 0 | <i>Epinephelus merra</i> , USNM 309689, 75.5 | 1 |
| Mullidae | | <i>Grammistes sexlineatus</i> , USNM 166994, 62.0 | 1 |
| <i>Mulloidichthys martinicus</i> , MPM 5321, 86.0 | 3 | <i>Hypoplectrodes</i> sp., USNM 198811, 67.5 | 1 |
| <i>Parupeneus multifasciatus</i> , MPM 13530, 79.0 | 3 | <i>H. maccullochi</i> , USNM 42039, 102.1 | 1 |
| <i>Upeneus maculatus</i> , USNM 126150, 76.0 | 3 | <i>Hypoplectrus puella</i> , MPM 23461, 92.3 | 1 |
| Nemipteridae | | <i>Liopropoma rubre</i> , MPM 25083, 41.0 | 1 |
| <i>Pentapodus porosus</i> , BMNH 1984.8.20:27, 62.0 | 0 | <i>L. sp.</i> , USNM 322359, 76.5 | 1 |
| Notograptiidae | | <i>Mycteroperca florida</i> , USNM 176238, 59.7 | 1 |
| <i>Notograpus</i> sp., USNM 173797, 174.0 | 2 | <i>Nippon spinosus</i> , USNM 59739, 130.0 | 1 |
| Opistognathidae | | <i>Paralabrax clathratus</i> , USNM 54807, 53.0 | 1 |
| <i>Opistognathus maxillosus</i> , MPM 30098, 98.3 | 2 | <i>Plectranthias nanus</i> , USNM 288812, 24.9 | 1 |
| Oplegnathidae | | <i>Pseudanthias taeniatus</i> , USNM 279782, 54.5 | 1 |
| <i>Oplegnathus fasciatus</i> , BMNH 1905.6.6:154–161, 126.0 | 0 | <i>P. thompsoni</i> , USNM uncat., 118.0 | 1 |
| Ostracoberycidae | | <i>Pseudogramma</i> sp., USNM 245340, 42.8 | 1 |
| <i>Ostracoberyx</i> sp., USNM 307282, 83.0 | 0 | <i>Serranus hepatus</i> , USNM uncat., 73.0 | 1 |
| Pempheridae | | <i>S. tigrinus</i> , MPM 30183, 58.3 | 1 |
| <i>Parapriacanthus ransonneti</i> , MPM 31028, 58.2 | 0 | Sillaginidae | |
| <i>Pempheris schomburgki</i> , FMNH 93774, 52.3 | 0 | <i>Sillago cilliata</i> , USNM 207647, 72.6 | 2 |
| Percichthyidae | | Siniperceidae | |
| <i>Percichthys altispinnis</i> , USNM 163382, 70.1 | 0 | <i>Coreoperca kawanebari</i> , USNM 71331, 32.3 | 2 |
| <i>Percilia gillissi</i> , USNM 84341, 60.0 | 0 | <i>Siniperca chautsi</i> , USNM 87082, 93.2 | 2 |
| Percidae | | Sparidae | |
| <i>Etheostoma nigrum</i> , MPM 22420, 56.3 | 1 | <i>Diplodus bermudensis</i> , MPM 18228, 76.5 | 0 |
| <i>Perca flavescens</i> , MPM 25409, 79.0 | 1 | Symphysanodontidae | |
| <i>Percina maculata</i> , MPM 20880, 76.7 | 1 | <i>Symphysanodon berryi</i> , USNM 289922, 85.5 | 0 |
| <i>Stizostedion canadense</i> , MPM 6015, 86.7 | 1 | <i>Synagrops bella</i> , USNM 156955, 75.5 | 2 |
| Pholidichthyidae | | Terapontidae | |
| <i>Pholidichthys leucotaenia</i> , USNM 289924, 77.0 | 2 | <i>Terapon jarbua</i> , USNM uncat., 80.0 | 0 |
| Plesiopidae | | Toxotidae | |
| <i>Acanthoclinus fuscus</i> , USNM uncat., 77.7 | 2 | <i>Toxotes jaculator</i> , USNM uncat., 45.0 | 0 |
| <i>Assessor macneilli</i> , USNM 295659, 40.5 | 0 | Scombroidei | |
| <i>Belonepterygion fasciolatum</i> , USNM 273813, 34.0 | 0 | Scombridae | |
| <i>Calloplesiops altivelis</i> , USNM 261333, 60.4 | 0 | <i>Scomber japonicus</i> , AMNH 74945, 149.0 | 0 |
| <i>Plesiops coeruleolineatus</i> , USNM uncat., 45.5 | 0 | Sphyraenidae | |
| <i>Trachinops taeniatus</i> , USNM 274580, 37.2 | 0 | <i>Sphyraena barracuda</i> , MPM 11496, 93.0 | 0 |
| Polynemidae | | Trichiuridae | |
| <i>Polydactylus approximans</i> , USNM uncat., 60.2 | 0 | <i>Trichiurus lepturus</i> , MPM 8430, 316.0 | 0 |
| Polyprionidae | | Scorpaenoidei | |
| <i>Polyprion americanus</i> , BMNH 1845.6.22:11, 190.0 | 0 | Agonidae | |
| Pomacanthidae | | <i>Agonus decagonus</i> , USNM 165146, 132.5 | 1 |
| <i>Centropyge bispinosus</i> , USNM 259696, 61.5 | 0 | Anoploplatidae | |
| Pomatomidae | | <i>Anoplopoma fimbriata</i> , USNM 208296, 123.0 | 1 |
| <i>Pomatomus saltatrix</i> , BMNH 1967.2.1:80–85, 74.7 | 0 | Aploactinidae | |
| Priacanthidae | | <i>Aploactis milesii</i> , USNM 59980, 121.0 | 1 |
| <i>Priacanthus hamrur</i> , USNM 289285, 72.5 | 0 | Bathylutichthyidae | |
| Pseudochromidae | | <i>Bathylutichthys taranetzi</i> , BMNH 1994.7.22:1, 100.5 | 0 |
| <i>Haliophis guttatus</i> , USNM uncat., 137.5 | 2 | Caracanthidae | |
| <i>Labracinus cyclophthalmus</i> , USNM 309335, 85.8 | 2 | <i>Caracanthus maculatus</i> , USNM 140990, 34.5 | 1 |
| <i>Ogilbyina queenslandiae</i> , USNM 290792, 59.3 | 2 | Congiopodidae | |
| <i>O. salvati</i> , USNM 278149, 50.3 | 2 | <i>Alertichthys blacki</i> , USNM 318386, 80.0 | 1 |
| <i>Pseudochromis elongatus</i> , USNM 290784, 35.6 | 2 | Cottidae | |
| <i>P. fuscus</i> , USNM 290345, 56.5 | 2 | <i>Ascelichthys rhodorus</i> , BMNH 1881.3.22:57–63, 50.0 | 1 |
| ' <i>Pseudochromis</i> ' <i>diadema</i> , USNM 290591, 32.9 | 2 | <i>Centrodermichthys analis</i> , BMNH 1890.11.15:105, 56.7 | 1 |
| Sciaenidae | | <i>Cottus bairdi</i> , MPM 5878, 70.8 | 1 |
| <i>Aplodinotus grunniens</i> , MPM 16805, 66.4 | 0 | | |

| Taxon, Catalogue No., SL (mm) | Type | Taxon, Catalogue No., SL (mm) | Type |
|---|------|--|------|
| <i>C. perplexus</i> , USNM 258839, 51.5 | 1 | <i>Kali normani</i> , USNM 207614, 159.6 | 0 |
| <i>Icelus hamatus</i> , BMNH 1877.5.13:7-9, 60.3 | 1 | <i>Pseudoscopus</i> sp., ARC 8706465, 57.0 | 0 |
| <i>Myoxocephalus scorpiis</i> , BMNH 1981.2.10:629, 50.5 | 1 | Creediidae | |
| <i>Taurulus bubalis</i> , BMNH 1981.2.20:776-794, 38.5 | 1 | <i>Crystalloides cookei</i> , FMNH 63619, 41.0 | 2 |
| Cottocomphoridae | | <i>Limnichthys fasciatus</i> , AMNH 57282, 45.5 | 2 |
| <i>Cottocomphorus grewingkii</i> , USNM 222075, 100.0 | 1 | Percophididae | |
| Cyclopteridae | | <i>Bembrops anatrostris</i> , AMNH 83323, 170.0 | 2 |
| <i>Cyclopterus lumpus</i> , USNM 197582, 83.8 | 1 | <i>B. gobioides</i> , FMNH 67070, 112.0 | 2 |
| Hoplichthyidae | | Pinguipedidae | |
| <i>Hoplichthys langsdorfi</i> , USNM 309447, 123.0 | 1 | <i>Parapercis cephalopunctatus</i> , FMNH 72471, 108.0 | 2 |
| Liparididae | | <i>P. montillai</i> , AMNH 50585, 94.0 | 2 |
| <i>Liparis agassizii</i> , USNM 74697, 117.5 | 1 | Uranoscopidae | |
| <i>L. liparis</i> , BMNH 1971.2.16:1757-1760, 99.5 | 1 | <i>Kathetostoma albiguttata</i> , FMNH 45246, 99.0 | 2 |
| <i>Paraliparis hystrix</i> , BMNH 1992.10.20:43-48, 87.8 | 1 | <i>Uranoscopus</i> sp., USNM 113145, 80.0 | 2 |
| Normanichthyidae | | Zoarcoidei | |
| <i>Normanichthys crockeri</i> , USNM 176507, 56.7 | 1 | Anarhichadidae | |
| Pataceidae | | <i>Anarrhichthys ocellatus</i> , USNM 57832, 585.0 | 2 |
| <i>Aetapcus maculatus</i> , BMNH uncat., 118.0 | 1 | Bathymasteridae | |
| <i>Pataecus fronto</i> , BMNH 1914.8.20:282, 159.0 | 1 | <i>Bathymaster signatus</i> , USNM 24004, 130.0 | 2 |
| Platycephalidae | | <i>Ronquilus jordani</i> , MPM 394, 133.1 | 2 |
| <i>Thysanophrys japonica</i> , USNM 70735, 119.0 | 1 | Stichaeidae | |
| Psychrolutidae | | <i>Anoplarchus purpureus</i> , MPM 366, 94.2 | 2 |
| <i>Cottunculus microps</i> , BMNH 1981.3.16:550-553, 87.5 | 1 | Zoarcoidei | |
| <i>Psychrolutes zebra</i> , BMNH 1986.7.12:193, 41.5 | 1 | <i>Lycodopsis pacifica</i> , MPM 408, 117.3 | 2 |
| Scorpaenidae | | PLEURONECTIFORMES | |
| <i>Pterois radiata</i> , USNM 140491, 64.8 | 1 | Achiridae | |
| <i>Scorpaena sonorae</i> , USNM 59463, 67.6 | 1 | <i>Achirus lineatus</i> , MPM 13783, 95.0 | 0 |
| <i>Sebastes alutus</i> , USNM 72461, 80.0 | 1 | Bothidae | |
| Triglidae | | <i>Bothus lunatus</i> , MPM 24885, 114.0 | 0 |
| <i>Bellator militaris</i> , USNM 114793, 83.0 | 1 | Cynoglossidae | |
| Stromateoidei | | <i>Symphurus plagiatus</i> , MPM 10525, 113.0 | 0 |
| Stromateidae | | Paralichthyidae | |
| <i>Peprilus burti</i> , MPM 8291, 92.4 | 0 | <i>Citharichthys spilopterus</i> , MPM 8951, 103.0 | 0 |
| Trachinoidei | | Pleuronectinae | |
| Ammodytidae | | <i>Pseudopleuronectes americanus</i> , AMNH 33401, 119.5 | 0 |
| <i>Ammodytes americanus</i> , AMNH 36780, 72.0 | 0 | Psettodidae | |
| <i>A. hexapterus</i> , FMNH 80613, 106.0 | 0 | <i>Psettodes erumei</i> , BMNH 1904.5.25: 197-8, 83.4 | 0 |
| <i>A. lanceolatus</i> , FMNH 34257, 177.0 | 0 | Poecilopsettinae | |
| <i>A. personatus</i> , USNM 104499, 86.0 | 0 | <i>Poecilopsetta hawaiiensis</i> , MPM 13604, 106.3 | 0 |
| Champsodontidae | | Samarinae | |
| <i>Champsodon</i> sp., USNM 150556, 64.2 | 1 | <i>Samariscus triocellata</i> , MPM 13387, 67.0 | 0 |
| Cheimarrichthyidae | | TETRAODONTIFORMES | |
| <i>Cheimarrichthys fosteri</i> , AMNH 98274, 71.0 | 1 | Balistidae | |
| Chiasmodontidae | | <i>Rhinecanthus aculeatus</i> , AMNH 50748, 52.5 | 2 |
| <i>Chiasmodon</i> sp., USNM 186139, 110.0 | 0 | Monacanthidae | |
| <i>Dysalotus alcocki</i> , MCZ 60806, 112.0 | 0 | <i>Pervagor pilosoma</i> , MPM 13528, 78.4 | 2 |

ing on to no other pterygiophores, but becoming continuous with the *supracarinalis posterior*. With such minimal fibre sharing of this elongate separate slip with the epaxial, it appears that the separate slip is likely to be a modified *supracarinalis posterior* or *supracarinalis medius*. Although no other taxon was found exhibiting this morphology, a few taxa do have a tendon extending to the *supracarinalis posterior* from the last fibres of the epaxial section that inserts on to the pterygiophores. We observed this condition in the cirrhitid *Paracirrhites arcaus*, some labrids (including *Sparisoma* and *Halichoeres*), as well as some blennioids. This tendon can be difficult to detect, and could be present in other taxa, although no trace of this feature was found in serranids or scorpaeniforms.

DISCUSSION

The insertion of epaxial muscle on to dorsal-fin pterygiophores is more widespread and exhibits more variation than has been previously reported. The distribution of the various recognized morphotypes suggests that it could have some value for estimating phylogenetic relationships. The most commonly encountered morphology among acanthomorphs, that of no epaxial insertions to dorsal posterolateral processes of dorsal-fin pterygiophores (Type 0), appears to be the primitive condition, as it occurs in all basal acanthomorph taxa (sensu Johnson & Patterson, 1993). Dorsal epaxial/ pterygiophore associations are absent from groups such as lampridiforms, polymixiiforms, basal paracanthopterygians, beryciforms, and smegmamorpha, as well as pleuronectiforms (Table 1). Hence, Types 1-3 are apomorphic at some level.

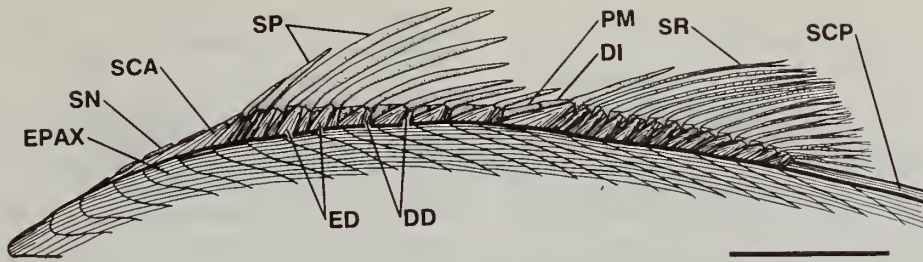


Fig. 1 Type 0 epaxial muscle as exemplified by *Morone chrysops* (MPM 4569, 78.8 mm SL). *Inclinatores dorsales* removed to expose medial muscles. Note that there is no insertion of the epaxial musculature to the distal tips of the pterygiophores. Margins of muscle demarcated by thicker lines; bone stippled. DD, *depressores dorsales*; DI, distal radial; ED, *erectores dorsales*; EPAX, *epaxialis*; PM, proximal-middle radial; SCA, *supracarinalis anterior*; SCP, *supracarinalis posterior*; SN, supraneural; SP, spines; SR, segmented ray. Scale bar = 10 mm.

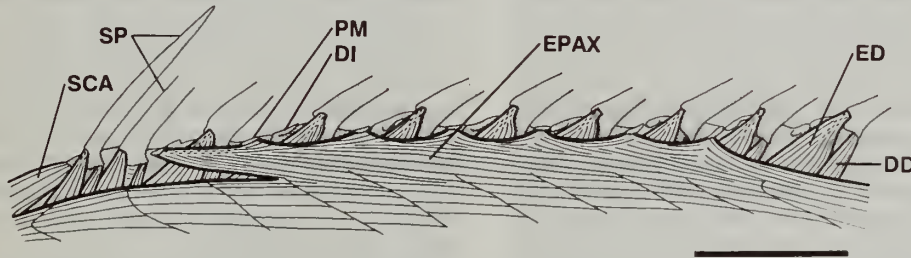


Fig. 2 Type 1 epaxial muscle as exemplified by *Epinephelus merra* (USNM 246689, 96.5 mm SL). *Inclinatores dorsales* removed to expose medial muscles. Note the separate slip of epaxial muscle which inserts dorsally on to the second pterygiophore (directly behind the second spine) and the additional insertions on to pterygiophores 3–8. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 5 mm.

Among these apomorphic morphologies, Type 1 is the easiest to characterize and identify. It is found among a restricted group of perciform families and is considered the exclusive epaxial/pterygiophore association of the Scorpaeniformes (see below for discussion of Type 0 condition in *Bathylutichthys*). A scorpaeniform sister group has remained elusive and this has been a serious barrier to understanding internal relationships of the Scorpaeniformes. The presence of a derived Type 1 epaxial morphology in the Scorpaeniformes and a small subset of the Perciformes suggests that the sister group of the Scorpaeniformes possibly lies within this subset. Percoid taxa rarely have been considered candidates for such status, although seven percoid families exhibit a Type 1 morphology (Table 1; Figs 2, 4–5). Despite generally being recognized as a heterogeneous and probably non-monophyletic assemblage (e.g. Johnson, 1984), percoids have been referred to as a single, identifiable taxonomic

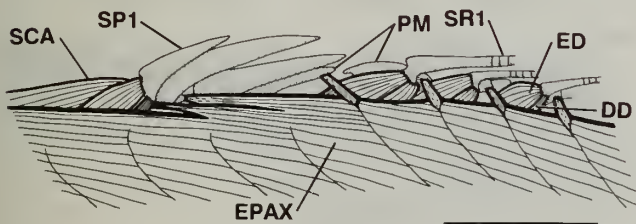


Fig. 3 Type 1 epaxial musculature in the batrachoid *Opsanus beta* (MPM 8919, 139.5 mm SL). Insertions to the 11th dorsal-fin pterygiophore. SP1, first spine; SR1, first segmented ray; other abbreviations and methods of presentation as in Fig. 1. Scale bar = 10 mm.

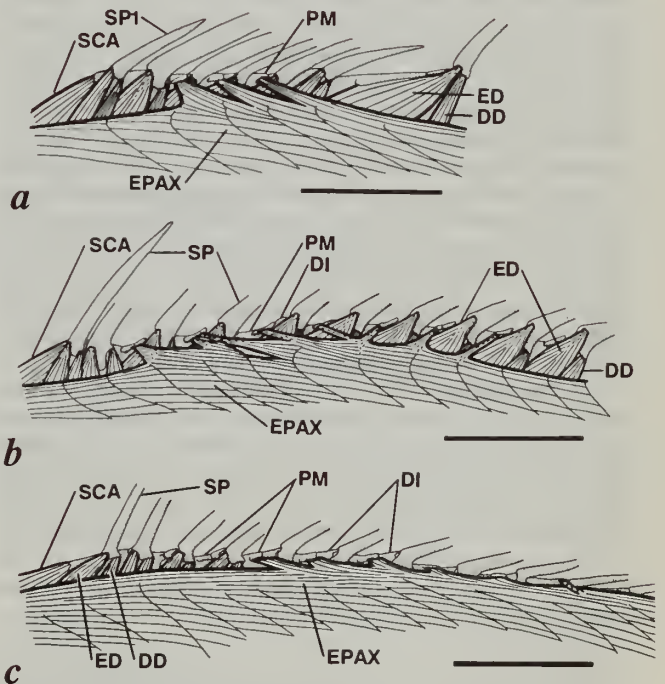


Fig. 4 Type 1 epaxial musculature in three percoids: *a*, *Apogon maculatus* (MPM 24869, 64.6 mm SL), Apogonidae, with insertions to the first through third pterygiophores; *b*, *Centrogenys vaigiensis* (USNM 150792, 53.4 mm SL), Centrogeniidae, with insertions to the first through seventh pterygiophores; *c*, *Perca flavescens* (MPM 25409, 79.2 mm SL), Percidae, with insertions to the fourth through ninth pterygiophores. Abbreviations and other methods of presentation as in Figs 1, 3. Scale bars = 5 mm.

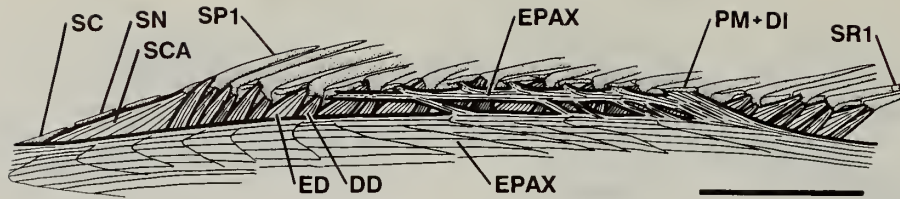


Fig. 5 Type 1 epaxial morphology with extreme fibre separation from the main epaxial body of the epaxial muscle slip inserting on to pterygiophores in *Haemulon aurolineatum* (MPM 23228, 64.2 mm SL). SP1, first dorsal-fin spine; SR1, first segmented dorsal-fin ray; other abbreviation and methods of presentation as in Figs 1, 3. Scale bar = 5 mm.

group for so long that they have been reified; in practice, most systematists regard the Percoidae as a bona fide taxon. As a consequence ichthyologists have rarely examined taxa from among the Percoidae as potential relatives of non-percoid taxa (exceptions include Johnson, 1984, 1986, 1993; Tyler *et al.* 1989), and few characters have been identified to suggest a relationship among percoids and scorpaeniforms, at least in part because few researchers have looked. These same problems apply to the more inclusive Perciformes, for which no satisfactory definition exists and membership is often questionable; families considered perciforms are rarely examined as either sister taxa or possible members of other acanthomorph orders (although see Johnson & Patterson, 1993) because, in practice, the Perciformes is treated as a monophyletic taxon.

Several additional characters suggest that a relationship between scorpaeniforms and at least some of the 'percoids' with a Type 1 epaxial morphology is worthy of consideration. For example, some larval serranids (particularly anthiines) bear at least a superficial resemblance to larval scorpaeniforms, with suspensorial and cranial bones highly ornamented by spines and ridges (cf. Figs and descriptions in: Baldwin, 1990; Johnson, 1984; Kendall, 1984; Washington *et al.*, 1984). Moreover, the general physiognomies of many adult serranids bear striking resemblances to certain scorpaeniforms. Although general similarities do not provide the necessary evidence for relationship, they hint that there might be more evidence than shared epaxial morphology; we feel it is premature to dismiss these similarities as being due to convergence before relationships are better understood.

The occurrence of Type 1 epaxial morphology in few non-percoid perciform taxa (blennioids, some cirrhitoids and some trachinoids) suggests that these should also be included in a search for a scorpaeniform sister group, or considered for inclusion among scorpaeniforms (Mooi & Johnson, in prep.). For example, blennioids also resemble scorpaeniforms in having the supratemporal sensory canal enclosed by the parietal (except in most tripterygiids where the cephalic sensory canals are incompletely enclosed by bone; Springer, 1993:487 and pers. obs.). This condition is found in several other perciform taxa, including at least some zoarcoids (sensu Anderson, 1984; Travers, 1984b; all 'zoarceoids' according to Gosline, 1968:46), some pseudochromids (Gill, in prep.), and mastacembeloid synbranchiforms (Travers, 1984a), but these taxa do not have a Type 1 epaxial morphology. Champsodontids more closely resemble scorpaeniforms in having a serrate ridge overlying the canal (Johnson, 1993:14; Mooi & Johnson, in prep.), as well as Type 1 epaxials. Although blennioid parietals lack the serrate ridge or spine over the canal, the possibility of a blennioid/scorpaeniform relation-

ship deserves further study. Certain cottoids closely resemble blennioids in dorsal gill arch morphology, notably in lacking an interarcual cartilage, and in having only a single infrapharyngobranchial (infrapharyngobranchial 3), which articulates posteriorly with epibranchials 3 and 4 (e.g., compare cottoids in Rosen & Patterson, 1990: figs 34A, C and Yabe, 1985: figs 23, 24E with blennioids in Rosen & Patterson, 1990: figs 33A–B, 37, 38C–D and Springer, 1993: fig. 1). Members of the cottoid family Liparididae further resemble blennioids in lacking an uncinat process on epibranchial 1 (Kido, 1988: figs 12A–D).

Johnson & Patterson (1993: 591) found no evidence to indicate a 'pre-perciform' position for scorpaeniforms, and considered ranking them at the subordinal level within the perciforms, 'if only to stimulate the search for characters justifying their individuality.' We concur with Johnson & Patterson's proposal and award subordinal ranking for the Scorpaeniformes, as the Scorpaenoidei, within the Perciformes. In addition to the justification provided by Johnson & Patterson (1993), we believe this action will be a major step forward in diagnosing a monophyletic Perciformes. There is no contrary evidence for maintaining the two orders as separate, and the epaxial morphology and other evidence noted above suggests that the Perciformes is non-monophyletic without the inclusion of the Scorpaeniformes.

The almost universal occurrence of Type 1 epaxial muscles in the Scorpaenoidei has implications for its composition. It casts doubt on the inclusion of the Dactylopteridae and Bathylutichthyidae within the suborder, as neither family has insertions of epaxial muscle to dorsal-fin pterygiophores (Table 1). Johnson (1993: 7) also raised doubts about a relationship between dactylopterids and scorpaenoids based on the absence of a bone-enclosed supratemporal canal and

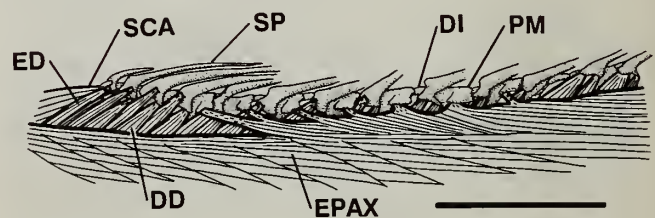


Fig. 6 Type 1 epaxial musculature in a 'primitive' scorpaeniform *Anoplopoma fimbriata* (USNM 208296, 122.2 mm SL). Note the separate slip of epaxial muscle to the third dorsal-fin pterygiophore, and other insertions of epaxial to as far posteriorly as the ninth pterygiophore. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 5 mm.

lack of parietal spines; Johnson & Patterson (1993: 579) considered and rejected a relationship between dactylopterids and gasterosteiforms. The monotypic family Bathylutichthyidae was recently erected by Balushkin & Voskoboinikova (1990) and placed in the Scorpaeniformes (our Scorpaenoidei) largely on the basis of trend characters variably shared with some cottoid taxa. Although *Bathylutichthys* could have secondarily lost Type 1 epaxial insertions, its position in the Scorpaenoidei should be regarded as provisional. The condition of the parietal and supratemporal canal in *Bathylutichthys* could be informative, but requires investigation.

Conversely, Mandrytsa (1991) has recently questioned the inclusion of the Pataecidae in the Scorpaenoidei (his Scorpaeniformes) based on a study of cephalic lateral-line structure. We have examined specimens of two of the three pataecid genera (*Aetapcus* and *Pataecus*; Table 1) and found that they have a typical scorpaenoid Type 1 arrangement of their epaxial musculature, corroborating their current position in the suborder. Ishida's (1994) more detailed analysis of various myological and osteological characters also conclusively nests pataecids within the Scorpaenoidei (as the sister group of the Aploactidae).

Winterbottom (1993) suggested a relationship of gobioids with the scorpaenoid family Hoplichthyidae, but this is not supported by our observations. Gobioids have no association of epaxial muscle with distal portions of the dorsal-fin pterygiophores, whereas hoplichthyids exhibit a typical scorpaenoid Type 1 pattern.

The shared Type 1 morphology in a subset of perciforms (blennioids, some cirrhitids, Apogonidae, some Centropomidae, Centrogeniidae, Champsodontidae, Cheimarrichthyidae, Grammatidae, Haemulidae, Percidae, and Serranidae) implies that closer relationships might exist among these taxa than are presently recognized (cf. Figs 2, 4-5, 12-17). The enigmatic family Centrogeniidae is an interesting example because its nomenclatural history reflects the possible relationships suggested by epaxial morphology. *Centrogenys waigiensis*, the single included species, and/or its junior synonyms, has variously been classified as a scorpaeniform (e.g., Day, 1875; Fowler & Bean, 1922), a serranid (e.g., Jordan, 1923; Weber & de Beaufort, 1931; Paxton *et al.*, 1989), or has been suggested to bear a superficial resemblance to cirrhitids (Gosline, 1966; Nelson, 1984). Although *Centrogenys* does not fit comfortably into any of these taxa as they are currently diagnosed, the similar Type 1 epaxial musculature suggests that a detailed anatomical comparison could provide considerable insight into their interrelationships.

In the Centropomidae, we found that extant members of

the subfamily Latinae (*Lates*, *Psammoperca*) have a modified Type 1 epaxial morphology where the muscle insertions to the pterygiophores are separate from the main epaxial body, but are below the spine/pterygiophore articulation (Fig. 12); this arrangement could also be described as a modified Type 0 morphology with a more dorsal position of the normally proximal insertions. The Centropominae (*Centropomus*) differ in lacking such dorsal epaxial insertions to dorsal-fin pterygiophores (Type 0) (Table 1). Greenwood (1976) hypothesized the monophyly of the Centropomidae, with its two subfamilies as sister taxa, on the basis of two synapomorphies: pored lateral-line scales extending to posterior margin of caudal fin, and neural spine of second vertebra markedly expanded in an 'anteroposterior direction.' Pored lateral-line scales extend well on to the caudal fin in many acanthomorph fishes, and reach, or nearly reach, the posterior margin of the fin in several families, including sciaenids (Greenwood, 1976), moronids (G.D. Johnson, pers. comm.), most pempheridids, rhyacichthyids (Springer, 1983) and polynemids. Therefore, this character does not provide convincing evidence of relationship, and may be plesiomorphic within perciforms. We also are not convinced that Greenwood's second character (also noted by Gosline, 1966), expansion of the second neural arch, is homologous in centropomines and latines. In adult centropomines (see Fraser, 1968: 455 for discussion of ontogenetic variation), the second neural spine is broadly expanded over most of its length (resulting in a truncated or rounded distal tip to the spine) and closely applied to the first neural spine, which is narrow and sharply pointed (see Fraser, 1968: fig. 14; Greenwood, 1976: fig. 25d; Rosen, 1985: fig. 39B). In contrast, the anterior neural spine morphology of the latines does not differ markedly from the conditions found in various basal perciforms; the second neural spine is only expanded proximally, and is not closely applied to the first neural spine (see Greenwood, 1976: figs 25a-c). Given the lack of convincing synapomorphies to unite the subfamilies Latinae and Centropominae, and considering the differences in epaxial morphology (as well as various other anatomical differences listed by Greenwood, 1976), there is no justification for placing them in a single family. Based on their modified Type 1 epaxial morphology, we here remove the African/Indo-Australian genera *Lates* and *Psammoperca* from the Centropomidae to a separate family, Latidae. *Hypopterus* (Western Australia) and *Eolates* (Italy [Monte Bolca]), included as latines by Greenwood (1976), presumably also belong to the newly created Latidae. Greenwood (1976) considered *Psammoperca macroptera*, the type species of *Hypopterus*, to be a synonym of *P. waigiensis*, the single species he recognized in *Psammoperca*; however, recent authors (e.g., Allen & Swainston, 1988: 62; Paxton *et*

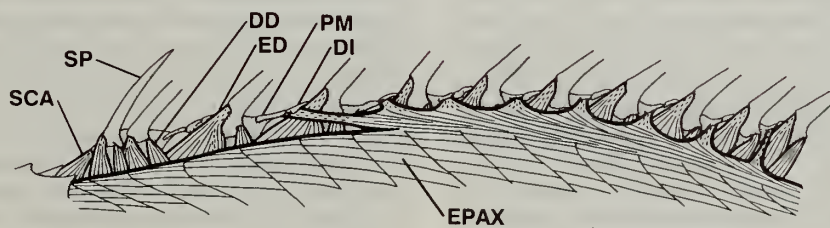


Fig. 7 Type 1 epaxial musculature in the scorpaeniform *Pterois radiata* (USNM 140493, 63.3 mm SL). Note the insertion of the epaxial muscle on to elements of the second pterygiophore and those posterior to the ninth pterygiophore. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 5 mm.

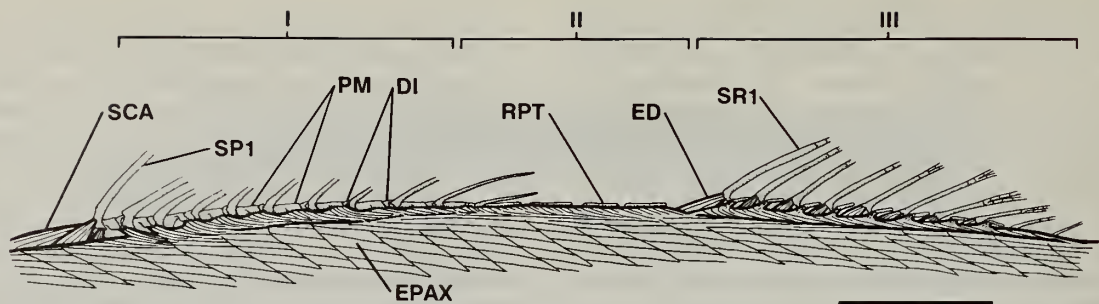


Fig. 8 An unusual Type 1 epaxial morphology in *Normanichthys crockeri* (USNM 176507, 63.4 mm SL). I – portion of the epaxial that inserts on to the anterior pterygiophores largely separate from the main body of the epaxial, with only a few fibres shared from each myoseptal section. The exceptions are the insertions on the two anteriormost pterygiophores which have many of their fibres originating from the main epaxial muscle body. II – portion inserting on to pterygiophores that is not separate from the main epaxial body. III – portion inserting on to the pterygiophores bearing segmented rays, is mostly separate until just beyond the last ray where it merges with the rest of the epaxial musculature. RPT, rayless pterygiophore; other abbreviations and methods of presentation as in Figs 1, 3. Scale bar = 5 mm.

al., 1989: 482) have regarded *Hypopterus* as a valid, monotypic genus. We provisionally retain the Centropomidae (*Centropomus* only) until its relationships are better understood.

The Trachinoidei as defined by Pietsch & Zabetian (1990) exhibit a variety of epaxial morphologies (Table 1). Ammodytids and chiasmodontids have Type 0, champsodontids and cheimarrichthyids have Type 1, and Type 2 is found in the creediids, percophidids, pinguipedids and uranoscopids. Considering the discussion by Johnson (1993: 13–15), this epaxial character distribution casts further doubt on the integrity of this suborder as currently constituted. Although it seems likely that the epaxial morphologies as defined here have evolved more than once among acanthomorphs, it is difficult to reconcile their distribution with the phylogeny provided by Pietsch & Zabetian (1990). One of their phylogenetic hypotheses is a sister group relationship between the Chiasmodontidae and the Champsodontidae. The Chiasmodontidae do not exhibit any muscle insertions on the dorsal-fin pterygiophores, whereas the Champsodontidae have a Type 1 condition very similar to that of scorpaenoids and serranids. Ammodytids, considered a derived trachinoid group, exhibit the primitive Type 0 condition, while a putative basal taxon, *Cheimarrichthys*, has Type 1, usually a derived morphology. Reversals are possible and structural homologies are uncertain (as discussed below), but the inconsistencies among these taxa suggest a more thorough investigation of the composition of the Trachinoidei sensu Pietsch & Zabetian (1990) is warranted.

There are differences even among those trachinoids that share a Type 2 morphology. *Parapercis* has a separate muscle that runs the entire length of the dorsal fin, with only intermittent epaxial fibres contributing to the muscle body. The posterior end of this separate muscle has some fibre and fascia connection with the *supracarinalis posterior* and only very weak attachments to the dorsal-fin pterygiophores that bear segmented rays. These pterygiophore insertions become strong anteriorly on spine-bearing pterygiophores, and the muscle is continuous with the *supracarinalis anterior*. This morphology is reminiscent of that of the Mullidae, described above, but shows an even closer association with the *supracarinalis* muscles, suggesting a *supracarinalis* derivation, rather than an epaxial one, for these pterygiophore insertions. This is completely different from the condition in

percophidids (*Bembrops*), which have a more typical Type 2 morphology with epaxial insertions on to the five pterygiophores of the anterior dorsal fin and to the first pterygiophore of the second, and with the anterior and posterior *supracarinalis* muscles entirely separate from the epaxial musculature. Of course, such differences can be interpreted as autapomorphies for families and genera among the trachinoids, but can also be considered suggestive of non-relationship.

Epaxial/pterygiophore associations can also strengthen hypotheses about monophyly of currently recognized groups. Although not unique among perciforms, the occurrence of the Type 1 attachment in *Niphon spinosus* (Fig. 13) and its proposed relatives, the serranids, lends support to Johnson's (1983) placement of *Niphon* within this family based on other characters. *Niphon* had previously been aligned with the Percichthyidae, a family that exhibits Type 0 epaxial morphology.

Among blennioids (sensu Springer, 1993), the Type 1 epaxial morphology has been found in all examined taxa, but there is some variation in details. Tripterygiids, dactyloscopids, clinids, chaenopsids and blenniids have a separate, more-or-less fan-shaped, anterior slip of the epaxial muscle bundle that inserts on to the distal portions of the anterior dorsal-fin pterygiophores and extends forward to the skull (Fig. 14a-c). We have not found this anterior slip elsewhere among acanthomorphs with epaxial attachments to dorsal-fin pterygiophores, and interpret it as a synapomorphy of the Blennioidei. This corroborates Springer's (1993) hypothesized monophyly of the suborder. However, labrisomids are an exception among blennioids in exhibiting a more typical Type 1 morphology, without an anterior slip to the skull (Fig. 14d). On the basis of molecular work, Stepien *et al.* (1993) hypothesized that the Labrisomidae are nested within the Blennioidei. Morphological characters provided by Springer (1993) also suggest that the Labrisomidae are not a basal blennioid family; for example, labrisomids, clinids, blenniids, and chaenopsids are more derived than tripterygiids and dactyloscopids in having the dorsalmost pectoral-fin ray articulating only with the dorsalmost proximal radial (vs with the scapula). Therefore, the absence of an anterior extension of the dorsal epaxial slip to the skull is most parsimoniously interpreted as a reversal, and a synapomorphy of the Labrisomidae.

It is also possible that the discovery of epaxial/

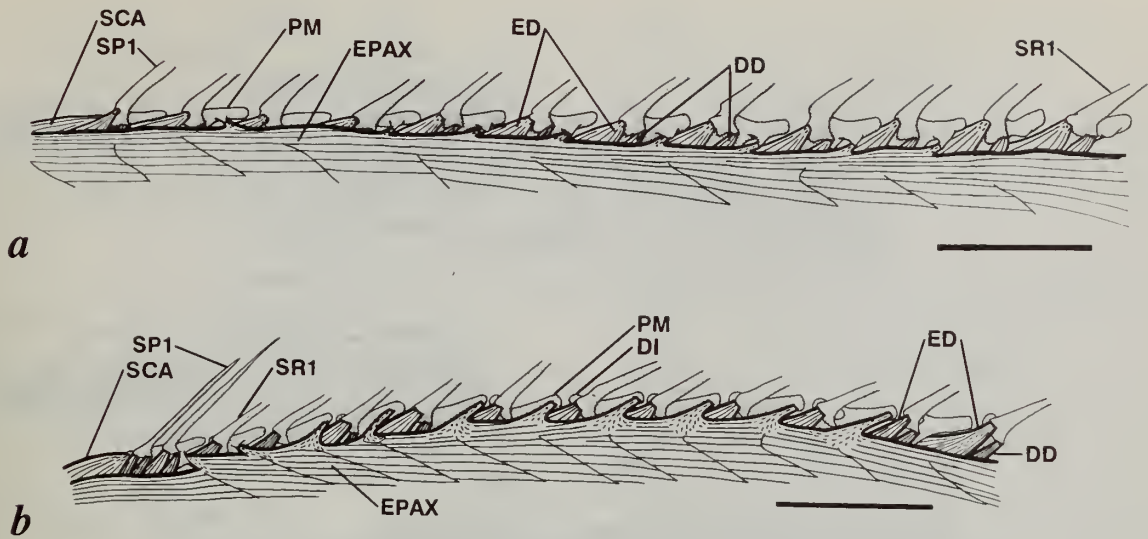


Fig. 9 Type 2 epaxial musculature as exemplified by: a, *Opistognathus maxilloxus* (MPM 30098, 98.3 mm SL); b, *Ronquilus jordani* (MPM 394, 133.1 mm SL). Abbreviations and other methods of presentation as in Figs 1, 3. Scale bars = 5 mm.

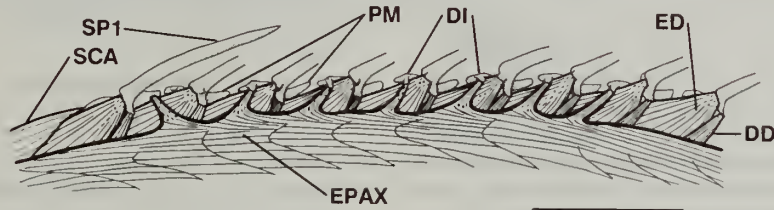


Fig. 10 Epaxial insertions via long tendons of *Sparisoma rubripinne* (MPM 30040, 62.6 mm SL), typical of some Type 2 epaxial muscles. Abbreviations and other methods of presentation as in Figs 1, 3. Scale bar = 5 mm.



Fig. 11 Type 3 epaxial musculature as exemplified by *Parupeneus multifasciatus* (MPM 13530, 79.0 mm SL). In contrast to Types 1 and 2, the dorsal epaxial has direct fibre insertion to only one anterior pterygiophore, and ventral to the articulation with the spine. These anterior fibres merge with what is possibly a modified *supracarinalis medius* (SCM?), which has a similar anterior insertion and tendinous insertions to a few posterior pterygiophores more dorsally. The epaxial muscle shares only a few fibres with the *supracarinalis medius* near the posterior end of the first dorsal fin. The *supracarinalis medius* is continuous with the *supracarinalis posterior*. SCM?, possible *supracarinalis medius*; other abbreviations and methods of presentation as in Figs 1, 3. Scale bar = 5 mm.

pterygiophore morphologies could help to determine the relationships of some of the *incertae sedis* genera of the Percoidei as identified by Johnson (1984; table 119). For example, *Siniperca* has Type 2 musculature, which, although a relatively common morphology, does circumscribe a smaller perciform group from which possible relationships could be initially explored. Johnson (1984) suggested a relationship between *Symphysanodon* and *Synagrops* based on larval morphology. We find the former taxon to have Type 0 and the latter to exhibit Type 2 epaxial morphologies. Although this does not refute a relationship, clearly more work needs to be done. Other orphan percoid genera such as *Lateolabrax* and *Haploxygnathys* have Type 0 morphology,

which suggests they are unlikely to be included among Type 1 taxa such as the Serranidae and Haemulidae (where each genus, respectively, had been traditionally placed).

Many percoid families have not had their close relatives identified. Epaxial morphology might limit the search for possible relationships for some of these taxa. For example, the Pholidichthyidae exhibit Type 2 morphology, and their relationships might be narrowed to other taxa with this morphology. Gill & Mooi (1993) summarized evidence suggesting a possible relationship of the Notograptidae to acanthocline plesiopids. Notograptidae and some acanthocline plesiopids share Type 2 morphology, which is absent in other plesiopids (Table 1), and this perhaps provides additional support for

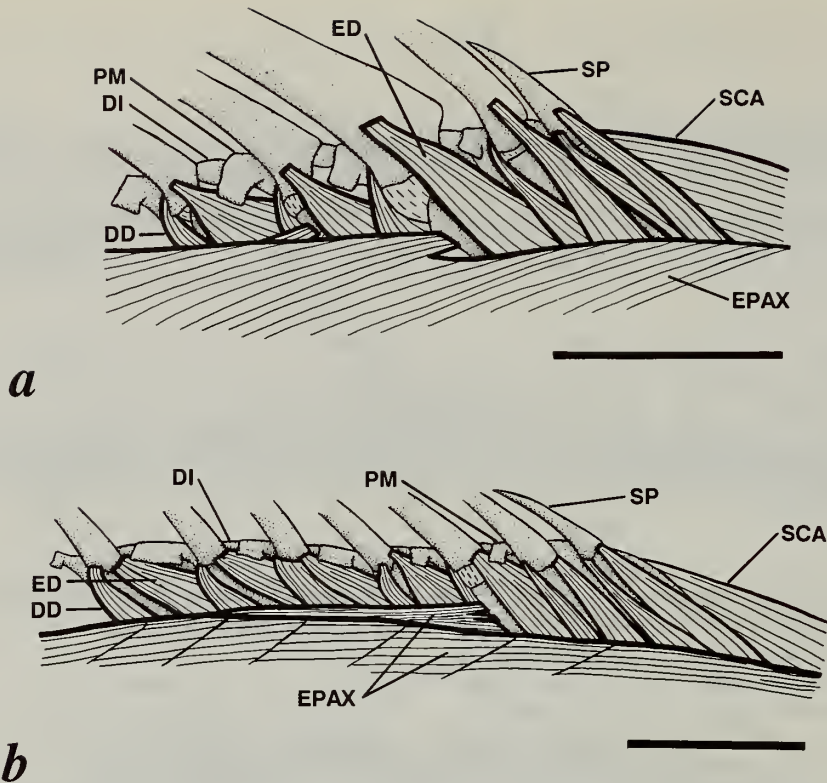


Fig. 12 Epaxial muscle morphology in: *a*, *Lates niloticus* (ROM 28524, 80.8 mm SL); *b*, *Psammoperca waigiensis* (ROM 46627, 91.2 mm SL). Note the insertions on to the second pterygiophore just ventral to the spine/pterygiophore articulation. Abbreviations and other methods of presentation as in Fig. 1. Scale bars = 5 mm.

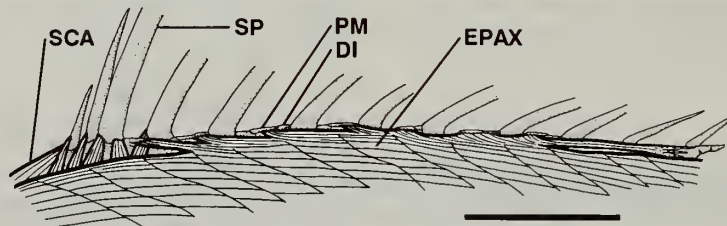


Fig. 13 Type 1 epaxial musculature in *Nippon spinosus* (USNM 59739, 128 mm SL). Note the separate slip of muscle inserting on to the second dorsal-fin pterygiophore and insertions to the 2nd through 8th pterygiophore, as in *Epinephelus* (Fig. 2). A separate bundle of fibres originates tendonously from the 10th pterygiophore to merge with those from the main epaxial muscle body. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 10 mm.

their relationship, or at least does not contradict such a conclusion.

Variation within families exhibiting a particular morphotype has considerable potential for exploring internal relationships. Among serranids, the anthiines *Hypoplectrodes*, *Acanthistius*, and *Plectranthias* all have very similar epaxial morphologies (Fig. 15), in which a short and not highly differentiated slip of muscle inserts on to the second pterygiophore, and a weak tendon extends from the myoseptum to the first pterygiophore. This differs notably from the condition in more typical anthiines, such as *Pseudanthias*, where a completely separate slip of epaxial muscle extends from below the fifth pterygiophore to insert on to the first through fourth pterygiophores (Fig. 16). These differences could provide evidence to unite members of one or another of these anthiine groups. If epinephelines are the sister group of anthiines as implied by Johnson (1988) and supported by

Baldwin & Johnson (1993), decisions concerning homology and character definition become crucial; primitive epinephelines (*Nippon*, *Epinephelus*) have a separate slip of muscle inserting on to the second pterygiophore, but no weak tendon to the first pterygiophore, a combination of features found in the two anthiine groups (cf. Figs 2, 13, 15, 16).

Variation in morphology of epaxial musculature might prove useful in other taxonomic groups. Insertion patterns of epaxial fibres to pterygiophores, the portions of the pterygiophore involved in the insertion, the degree of separation of the involved musculature from the main body of the epaxial, and the relationship of the muscle with the *supracarinalis* all vary. Among the haemulids examined, *Anisotremus* has a limited number of attachments involving only the fourth and fifth pterygiophores, *Conodon* exhibits a more robust continuous series of insertions extending from the third to seventh pterygiophores more typical of Type 1, and *Haemu-*

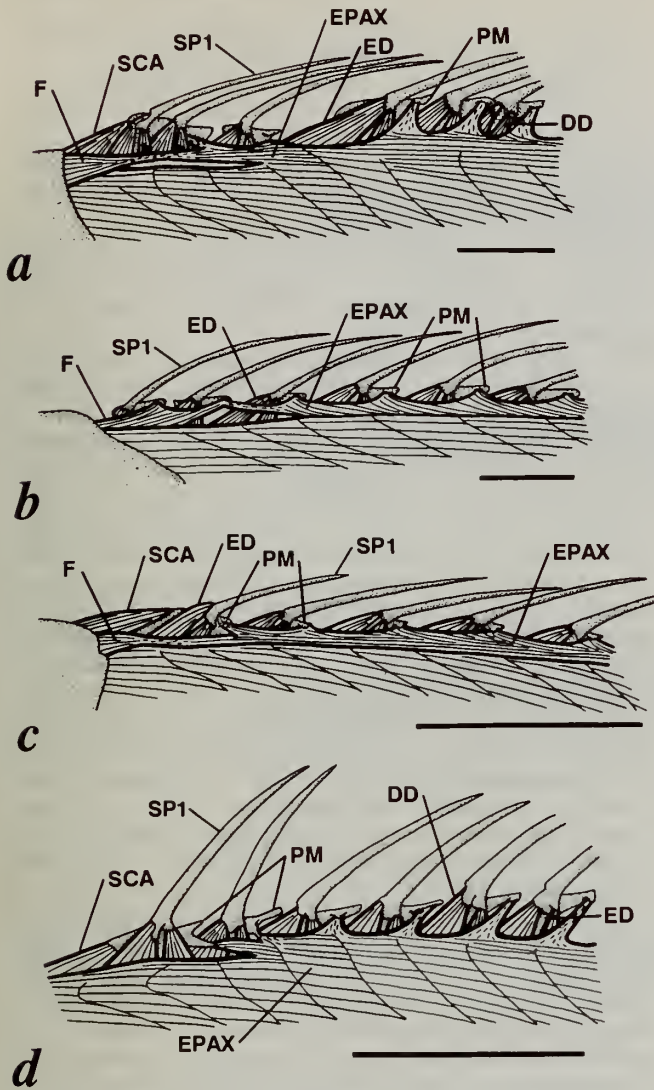


Fig. 14 Epaxial musculature of blennioids: a, Tripterygiidae, *Enneanectes pectoralis* (MPM 22463, 26.5 mm SL), insertions to ninth pterygiophore; b, Chaenopsidae, *Acanthemblemaria greenfieldi* (MPM 24876, 30.4 mm SL), insertions to 13th pterygiophore; c, Blenniidae, *Entomacrodus nigricans* (MPM 18256, 55.4 mm SL), insertions to 11th pterygiophore; d, Labrisomidae, *Labrisomus bucciferus* (MPM 31163, 57.0 mm SL), insertions to 13th pterygiophores. F, fan-shaped anterior slip of epaxial to skull; other abbreviations and methods of presentation as in Figs 1, 3. Scale bars = 1 mm (a,b), 5 mm (c,d).

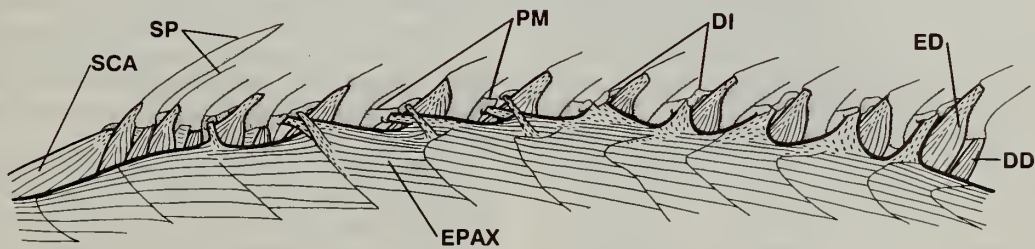


Fig. 15 Type 1 epaxial musculature in *Acanthistius sebastoides* (USNM 246689, 96.5 mm SL). A weak tendon extends from a myoseptum to the first pterygiophore and a short and not highly differentiated muscle slip inserts on to the second pterygiophore. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 5 mm.

lon has an almost completely separate series of muscle fibres that insert on to the third to ninth pterygiophores (Fig. 5). Type 1 appears to be the primitive condition for the cirrhitoids (Fig. 17), with a secondary change to an epaxial/pterygiophore association resembling more closely a Type 2 morphology among some cirrhitids, which could be indicative of close relationship (Table 1). Among sciaenids both epaxial muscle Types 0 and 2 occur, although their distributions are difficult to interpret with our current understanding of sciaenid relationships (Table 1; Sasaki, 1989). Within scorpaenoids there is variation in epaxial morphology among the higher taxa. More extensive surveys within these and other groups with epaxial/pterygiophore insertions could help to elucidate some of their intrarelationships.

Basal taxa (Embiotocidae, Pomacentridae, and Cichlidae) of the suborder Labroidei (Kaufman & Liem, 1982; Stiassny & Jensen, 1987) exhibits Type 0 morphology, whereas some labrid taxa exhibit Type 2 (Table 1). It is most parsimonious to interpret Type 2 epaxial muscle as independently derived within labrids. This interpretation places *Bodianus*, *Choerodon*, and *Tautoga* as basal genera among the Labridae, and might be helpful for determining the polarization of other characters for phylogeny reconstruction in this confusing group.

Some tetraodontiforms exhibit epaxial insertions on to the distal tips of the dorsal-fin pterygiophores that resemble Type 2: Balistidae (*Rhinecanthus*, pers. obs.; probably *Balistes*, *Balistapus*, *Melichthys*, and *Odonus* from figs 78, 86, 88 and 90 in Winterbottom, 1974b), Monacanthidae (*Pervagor*, pers. obs.; probably *Aluterus*, *Cantherines*, *Chaetoderma*, *Paraluteres*, *Paramonacanthus*, and *Stephanolepis* from figs 100, 102–105 and 108 in Winterbottom, 1974b), probably Triacanthidae (*Triacanthus*, *Tripodichthys*, *Trixiphichthys* from figs 66, 76–77 in Winterbottom, 1974b), and perhaps some Triacanthodidae (*Triacanthodes*, *Tydemania*, and *Macrorhamphosodes* but not *Hollardia* or *Parahollardia* from figs 49, 57–58, 61 and 64 in Winterbottom, 1974b). Consideration of the overall anterodorsal morphology of balistids, monacanthids, and triacanthids suggests that these insertions are likely to have been derived independently of (and non-homologous with) those found in the Perciformes. In these tetraodontiforms, the anterior spinous dorsal fin is closely associated with the back of the skull and separated from the soft dorsal fin. It seems that the robust pterygiophores of the spinous dorsal fin act functionally as a supraoccipital crest and that the epaxial musculature inserts on to these elements as it would to such a crest. If triacanthodids, which possess a more conventional arrangement of spinous dorsal fin and posterior skull, do have epaxial/dorsal pterygiophore inser-

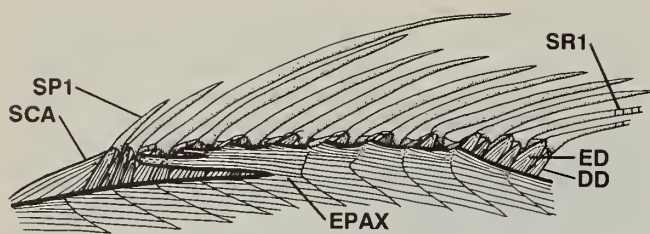


Fig. 16 Type 1 epaxial musculature in *Pseudanthias taeniatus* (USNM 279782, 44.8 mm SL). A separate slip of the epaxial inserts on to the first to fourth dorsal-fin pterygiophore, and epaxial insertions occur as far posteriorly as the eighth pterygiophore. Abbreviations and other methods of presentation as in Figs 1, 3. Scale bar = 5 mm.

tions, an argument could be made for homology with a Type 2 morphology found among the perciforms, and implied relationships should be investigated. Optimizing epaxial character distribution on existing phylogenies of the tetraodontiforms (Winterbottom, 1974b; Leis, 1984) implies that the Type 2 morphology is the primitive condition for the order. Unfortunately, the character does not provide additional evidence for intrarelationships because the remaining extant families of tetraodontiforms do not possess a spinous dorsal fin.

Even among taxa that do not exhibit epaxial insertions on to the distal portions of the proximal-middle pterygiophores or on to the distal radials, we did observe some possibly significant variation in other muscle morphology. As noted above, most (if not all) acanthomorphs have epaxial muscle insertions on to the proximal ends or along the shafts of the dorsal-fin pterygiophores. In most pleuronectiforms the epaxial muscle inserts via bundles of muscle fibres that pass underneath the *depressores dorsales*. *Psettodes*, usually considered the sister group of other pleuronectiforms, has the epaxial muscles overlying most of the length of the pterygiophores, with very short connections extending under the depressors to the pterygiophore shafts just ventral to the spine articulations. These connections only occur on the first 12 pterygiophores. *Psettodes* is the only genus with dorsal-fin spines; all other flatfishes have epaxial insertions on to a higher number of pterygiophores, although most of the examined taxa have dorsal fins extending over the head. The extent to which the epaxials overlie the pterygiophores in remaining flatfishes varies considerably and might be of interest for determining relationships. The few examined bothids, paralichthyids and samarines have the epaxials covering about half the length of the pterygiophores before short fibres attach to these bones. In available achirids the arrangement is similar to that described for bothids for the most posterior insertions, but anteriorly there are separate, elongate muscle slips that insert high on to the pterygiophore shafts just ventral to the ray articulations (Fig. 18). The cynoglossids, considered close relatives of the achirids (Chapleau, 1993), have an epaxial morphology more similar to that of *Psettodes* in the one species examined. *Poecilopsetta* (Poecilopsettinae) has epaxial muscles that lie only as far dorsally as the proximal tips of the dorsal-fin pterygiophores, a condition that appears derived among pleuronectiforms and could provide evidence for relationship if observed in other taxa. Additional taxa need to be surveyed and character definitions must be clarified before epaxial morphology can

contribute to an hypothesis of pleuronectiform phylogeny, but such an investigation appears worthy of pursuit.

A similar, though less extensive, series of epaxial insertions under the depressors is found in *Urophycis* of the Gadidae (Fig. 19). Gadoids have not been thoroughly surveyed, but variation in epaxial muscle morphology, which is relatively simple to observe, might be useful for defining broad groups among gadoids, and paracanthopterygians in general. The occurrence of a Type 1 epaxial morphology among batrachoidids also suggests that a further survey of paracanthopterygians could contribute to the understanding of relationships within this taxon.

Of course, epaxial muscle morphology is not informative in all cases. For example, the Callionymoidei have a highly modified Type 2 condition consisting of a complex series of epaxial insertions on to the pterygiophores and modified neural spines. This will not help determine whether the Callionymoidei and Gobiesocidae are sister taxa, as hypothesized by Gosline (1970) and Winterbottom (1993: 409), because the latter taxon does not have a spine-bearing dorsal fin. It would be reasonable to suggest that any epaxial muscle associated with the fin would also have disappeared or have become reduced. Like any other feature, epaxial morphology can undergo secondary loss or autapomorphic modification.

The homology of the three epaxial muscle morphotypes identified remains uncertain. It is unlikely that they form a nested set of character states. That a single morphotype can be independently derived from a Type 0 condition is illustrated by the independent development of Type 2 in some labrids, and similarly in the Acanthoclininae, a derived taxon within the Plesiopidae which otherwise exhibit Type 0 (Table 1). The occurrence of a Type 1 morphology in some paracanthopterygians, usually considered unrelated to perciforms, also indicates non-homology of the character state as recognized here. These examples suggest that the morphologies themselves require better definition. With more sophisticated inquiry through ontogenetic or neurological studies, it is possible that these cases of non-homology can be dismissed as inappropriately recognized character state equivalence. In the apparently unique morphology of the Mullidae, Type 3, the pterygiophore insertions involve both epaxial and *supracarinalis* fibres (Fig. 11). The muscle is essentially separate from the main epaxial muscle body over its entire length, a condition very different from that found in the Type 1 or 2 morphologies. It appears that the Type 3 musculature is directly derived from the *supracarinalis* muscles, rather than from the epaxial muscles. This also seems likely in the pinguipedid trachinoid *Parapercis*, where the muscle bundle inserting on to the dorsal-fin pterygiophores is continuous with the *supracarinalis anterior* and *posterior*. The condition in mullids and *Parapercis* could provide evidence that, in at least these taxa, the sheet of muscle inserting on to dorsal-fin pterygiophores is actually derived from the *supracarinalis*, and only secondarily shares muscle fibres from the *epaxialis*. These problems of homology and ontogeny of the muscle are beyond the scope of this paper.

Despite these concerns, we are confident that epaxial morphology is useful for exploring the relationships of acanthomorph taxa. Of course, this one character complex must be taken in the context of other characters before any definitive statements can be made regarding, for example, percoid/scorpaenoid relationships, or before making generalizations concerning the integrity of such groups as the trachinoids. However, one important concept that the inves-

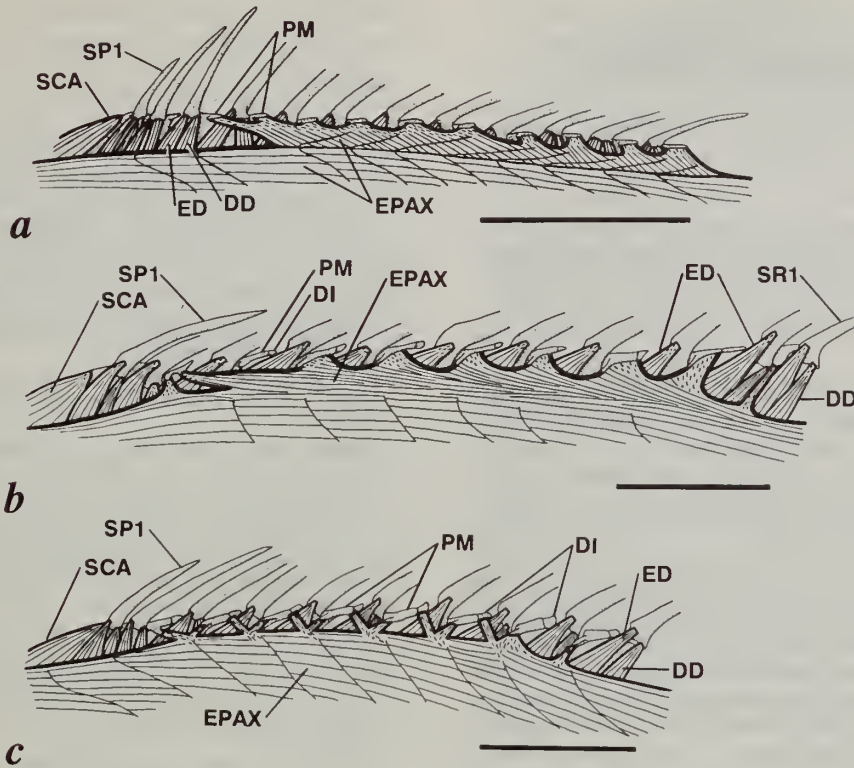


Fig. 17 Epaxial musculature in cirrhitoids: a, Type 1 in Aplodactylidae, *Aplodactylus punctatus* (USNM 227298, 58.0 mm SL); b, modified Type 1 in Cirrhitidae, *Paracirrhites arcatus* (MPM 13587, 66.7 mm SL); c, Type 2 in Cirrhitidae, *Amblycirrhites bimacula* (MPM 13509, 56.9 mm SL). Abbreviations and other methods of presentation as in Figs 1, 3. Scale bars = 5 mm.

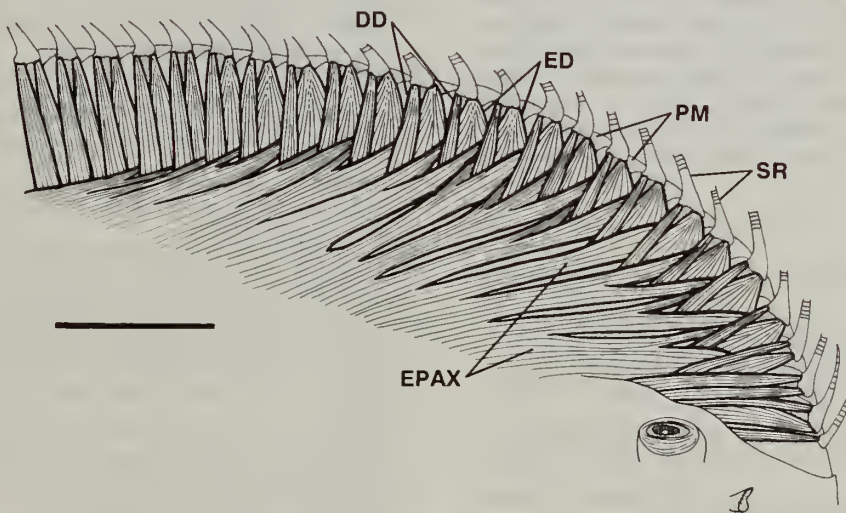


Fig. 18 Epaxial musculature of the pleuronectiform *Achirus lineatus* (MPM 13783, 95.0 mm SL). Individual slips of *epaxialis* insert on to the dorsal third of the dorsal-fin pterygiophore shafts under the *depressores dorsales*. Abbreviations and other methods of presentation as in Fig. 1. Scale bar = 10 mm.

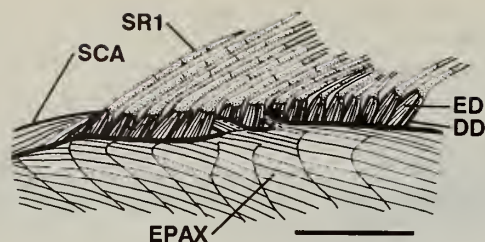


Fig. 19 Epaxial musculature in the gadid *Urophycis regia* (MPM 31175, 133.0 mm SL). Individual slips of muscle extend from the main *epaxialis* body to insert on the dorsal-fin pterygiophore shafts under the *depressores dorsales*. Abbreviations and other methods of presentation as in Figs 1, 3. Scale bars = 5 mm.

tigation of epaxial muscle variation elucidates is the need to shrug off the straitjacket of present classifications when investigating phylogeny of higher taxa. This is particularly true when the taxa are already recognized as non-monophyletic, undefined, or poorly defined (e.g., Percoidae, Perciformes, Paracanthopterygii), but have in essence been reified over time. It is necessary to look beyond the traditional taxonomic boundaries, not only when dealing with undefined groups such as the percoids, but also when investigating apparently well-defined or well-established taxa such as the scorpaenoids and trachinoids. Epaxial muscle insertions to dorsal-fin pterygiophores provide one character complex that illustrates the potential and novel relationships that such an approach can suggest. These possible relationships await rejection or corroboration from similar studies of additional characters.

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